Habitat Use and Small-Scale Residence Patterns of Sympatric Sunfish Species in a Large Temperate River

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Abstract

Bluegill (*Lepomis macrochirus*) and pumpkinseed sunfish (*Lepomis gibbosus*) function as a trophic link between invertebrates and piscivores in temperate freshwater food webs, but little is known about their movement in large-scale ecosystems. To address this, pumpkinseed and bluegill were implanted with acoustic transmitters and monitored for five months (June to November 2015) within a 0.39 km^2 acoustic array in the large Detroit River. Residence Index (RI) analysis revealed site fidelity of sunfish to the side of the river they were tagged and a lack of movement across a shipping channel. Bluegill were more active at night and pumpkinseed more active during daylight hours, possibly partitioning resources on a temporal basis, unlike in smaller lakes where the species partition the littoral and pelagic habitats. Pumpkinseed presence was positively correlated with water temperature and level, whereas bluegill presence was not related to any environmental parameters examined. This study demonstrates that anthropogenic alterations, e.g. channelization, influence the movement and distribution of fishes and that fish behaviour in a large river ecosystem can differ from smaller temperate lakes.

Keywords

Acoustic telemetry, spatial ecology, freshwater, sunfish, Great Lakes, Detroit River, diel variation

Introduction

Fish movements and distributions form the basis of the structure and functioning of aquatic ecosystems (Hussey et al. 2015). As a source of significant energy subsidies to food webs, the movements of forage fishes can influence the spatial and temporal distributions of predators, which has numerous implications for fisheries management typically focused on higher trophic level fishes that are part of recreational or commercial fisheries (Eklöv 1997). Knowledge regarding the small-scale movements of prey fishes and how they are related to environmental processes is important in understanding their role in food webs, the behaviour of piscivores, and predicting food web structure in general. A result of the influence of prey fish distributions could be the movement of fishes across biologically irrelevant boundaries, i.e. international borders, which may be common in large aquatic ecosystems, such as the Laurentian Great Lakes shared by Canada and the United States of America.

The Laurentian Great Lakes is composed of five large post-glacial lakes and major connecting channels in North America that play an important ecological and economic role in the region (Magnuson et al. 1997). For humans, this system is an essential inland shipping route, sustains recreational and commercial fisheries, and supplies water for domestic, agricultural, and industrial uses (Magnuson et al. 1997). This concentration of human activity in the Great Lakes region has resulted in numerous environmental challenges and stressors related to both indirect effects, e.g. pollution and runoff (Manny and Kenaga 1991), and direct alterations to physical habitat, e.g. channelization to facilitate movement of large-scale vessels (Bennion and Manny 2011). One of the drivers of human activity in the region is the unique ecological characteristics of this watershed. As the world's largest freshwater ecosystem, the lakes (Superior, Michigan, Huron, Erie, Ontario) and their connecting channels (St. Mary's River, St. Clair River, Lake St. Clair, Detroit River, Niagara River) support a diverse and unique range of freshwater fish species (Manny et al. 1988; Read et al. 2010; Hondorp et al. 2014). While studies have revealed the biological patterns of many freshwater fishes in smaller temperate lakes (Keast 1978*a*, 1978*b*; Colborne et al. 2015), the movement and behaviour of these species often remains relatively unknown in the Great Lakes, particularly in relation to areas of direct human alteration.

The Huron-Erie Corridor (HEC), consisting of the St. Clair River, Lake St. Clair, and the Detroit River, connects the upper and lower Laurentian Great Lakes, functioning as a major migration route, spawning and nursery area, and habitat for a number of freshwater fish species (Manny et al. 1988; Lapointe et al. 2010; Hondorp et al. 2014). The HEC exhibits some of the highest biodiversity in the entire Great Lakes region, possessing an abundance of species that interact in a complex food web (Manny et al. 1988; Thébault and Loreau 2005; Bennion and Manny 2011). Historically, the Detroit River supported an abundance of coastal wetlands and submerged macrophyte beds (Bennion and Manny 2011; Hondorp et al. 2014), which likely contributed to this river having the greatest overall biodiversity within the HEC (Francis et al. 2014). Through extensive modification and urbanization, their distribution has decreased, reducing habitats for fish and other wildlife (MacLennan et al. 2003; Hondorp et al. 2014). As a major shipping route, channelization related to the passage of large-scale freighters has established an artificially steep depth profile in the river. Data on the ecological patterns of all fish species, including forage fish that we define as linking invertebrate prey and higher trophic level piscivores in the Detroit River, will provide a more comprehensive understanding of the ecosystem dynamics as a whole, providing data relevant to ongoing restoration efforts currently occurring in the region (e.g. Hondorp et al. 2014) and to broader evidence-based decision making regarding aquatic communities in large river ecosystems.

Pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*) are two congeneric species of the Centrarchidae family with a spatial distribution that encompasses freshwater lakes in the northeastern United States and southern Canada (Mittelbach 1984). In many lakes, pumpkinseed and bluegill are sympatric and partition resources between littoral (e.g. benthic gastropods) and pelagic resources (e.g. zooplankton in the water column) as a result of interspecific competition and functional morphological differences between the species (Mittelbach 1984; Locke et al. 2013). Indeed, in lakes where only one of these species is found they often have foraging polymorphisms, i.e. ecotypes or ecomorphs, within the species that exploit littoral and pelagic resources differently (e.g. Ehlinger and Wilson 1988; Jastrebski and Robinson 2004; Colborne at al. 2016). Within the HEC, pumpkinseed and bluegill are common lower trophic level forage fish that consume a variety of resources ranging from benthic macroinvertebrates to zooplankton, while also falling prey to numerous piscivorous species throughout their life cycle (Mittelbach 1984; Wainwright 1996; Collingsworth and Kohler 2010). In general, sunfish function as secondary consumers within freshwater foodwebs. Species that commonly prey on pumpkinseed and bluegill include largemouth bass (*Micropterus salmoides*), bowfin (*Amia calva*), smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), walleye (*Sander vitreus*), and northern pike

(*Esox lucius*) (Jordan et al. 2009; Collingsworth and Kohler 2010; Nawrocki 2015). The role of pumpkinseed and bluegill as a link in the food webs of the Great Lakes emphasizes the significance of monitoring these smaller forage species, yet most studies of these species take place in small temperate lakes (e.g. Fish and Savitz 1983; Collingsworth and Kohler 2010; Berchtold et al. 2015), leaving questions about sunfish in larger lakes and rivers.

The spatial and temporal habitat use of pumpkinseed and bluegill can be passively monitored using acoustic telemetry. Passive biotelemetry is advantageous over active methods used to measure abundance and movement as it is less labour intensive, provides the possibility for continuous 24 h data collection, minimizes disturbances, and can simultaneously track multiple individuals with a single array of receivers (Kessel et al. 2014; Hussey et al. 2015). Through the application of acoustic telemetry, the specific aims of this study were to: (1) compare the spatial distribution of pumpkinseed and bluegill in a small region (0.39 km^2) of the Detroit River that has variable habitat (nearshore with high macrophytes and open water channel); and (2) determine if specific environmental variables and diurnal patterns are related to sunfish activity in these habitats in the Detroit River. To accomplish this, an acoustic telemetry array was set up in the Detroit River over a 5-month period within an area of the river containing macrophyte-rich areas separated by an open-water area produced through channelization. As a function of the unique morphology, depth profile and flow patterns related to channelization of the river, we predicted that both pumpkinseed and bluegill would inhabit the shallow littoral flats on either side of the shipping channel. We also predicted that interspecific variation would exist with pumpkinseed preferring more inshore regions and bluegill occupying more open water areas closer to the edge of the shallow flats, related to the foraging patterns observed in smaller waterbodies (Mittelbach 1984; Ehlinger and Wilson 1988; Berchtold et al. 2015). Of the many environmental parameters known to influence fish behaviour, migration and biology, including water temperature (e.g Jackson et al. 2001), water level (e.g. Rogers et al. 2005), moon illumination (e.g. Laroche et al. 1997), wind speed (e.g. Oviatt and Nixon 1973) and flow (e.g. Schlosser 1991), we expected that water temperature would influence the activity of both pumpkinseed and bluegill in the nearshore areas the most, as this variable has often been recognized to influence the behavior and movement of freshwater fish species on a variety of scales (e.g. Shuter et al. 1980; Grossman and Freeman 1987).

Methods

Study site

Forming the lower third of the Huron-Erie Corridor, the Detroit River spans a distance of 51 km (Manny and Kenaga 1991; Lapointe 2014). We chose a study site that is located within a secondary shipping channel near the mid-point of the river's run. The study site bordered LaSalle (Ontario, CAN) on the east shore of the Detroit River, and Fighting Island in the river that represented the western boundary. We designated an area approximately 600 m wide (LaSalle shoreline to Fighting Island shoreline) and 650 m long (42^{o}23N, 83^{o}10W; Fig. 1). Mean water depth in this area is < 9 m, which is shallower than upstream regions with depths of up to 15 m and exceeds historical water depths throughout the river that averaged 6.0 to 7.6 m (Manny and Kenaga 1991; MacLennan et al. 2003).

Acoustic telemetry array

An array of VR2W 180-kHz receivers (Vemco Ltd®, Nova Scotia, Canada) was established in the Detroit River to track the movement of tagged pumpkinseed and bluegill (Fig. 1). The array consisted of regularly spaced receivers (n = 26) on either side of the secondary shipping channel, hereafter channel, that extended outwards from the shore through the shallow vegetated flats, hereafter shallow, to the edge of the channel. The design of this array provided coverage of the regions sunfish typically inhabit while allowing for potential channel movements to also be detected. All receiver moorings were active as of 23 June 2015 at depths of 0.5 – 4 m and spaced 75 – 275 m apart. Receiver moorings were constructed by placing two PVC pipes into the openings of a concrete cinder block (~16 kg), filling the openings with concrete, and placing a piece of re-bar in the wet cement to create a handle. The second receiver slot was used to hold a VR2W 69-kHz receiver that is part of a broader acoustic telemetry project unrelated to the data presented here. For the purposes of this study, we analyzed detections from 24 June – 16 November 2015. Detection range within the shallow, densely vegetated portions of the study area was quantified and temporally monitored using a set of range test tags (see Supplemental material for details).

Fish collection and tagging

Sunfish were tagged over the course of three days: 23 – 24 June 2015 (pumpkinseed n = 16, bluegill n = 7) and again 6 August 2015 (pumpkinseed n = 3, bluegill n = 3). Fish were collected using a single anode boat electrofisher (Smith-Root 5.0 GPP) set to use pulsed DC current at 60 Hz (voltage 1 – 1000 V) using between 30 – 60% of the range to maintain a current of 6 – 8 A. As the boat moved through the study area at a slow speed, stunned fish were visually identified and captured by hand using dip nets on 1.5 m poles. Upon capture, fish were placed in a holding tank of fresh river water on the electrofishing boat for a maximum of 15 min before being transferred to a holding tank on the research boat where tagging was performed. Fish in the holding tank were placed in an anesthetic solution of tricaine methane-sulfonate (MS-222; 50 – 75 g MS-222 per 1 L water) until the fish lost their righting response and did not respond to stimuli. Total length (L_T) was measured to the nearest 1 mm and wet mass to the nearest 1 g. The fish were then placed in a cradle and provided with a stream of fresh river water to maintain water flow over their gills. A mid-ventral incision ~10 mm in length was made anterior to the pelvic fins on the left side and a Vemco V5-1x transmitter (360 – 440 s nominal transmission delay; max. tag life of 350 days) was inserted into the body cavity. Tag size was 4.3 x 12.7 mm and 0.65 (in air) – thus providing a tag to body weight ratio range of 0.4 – 2.0% for all specimens. The incision was closed with two independent sutures (Ethicon Coated VICRYL Plus Antibacterial size 5-0 with RB-1 tapered needle) tied with a 3-1-1 knot. All surgical equipment was cleaned in betadine solution (1 betadine : 9 water) prior to implanting each transmitter. Procedures lasted < 10 min from the fish being placed in the anesthetic bath to being put in the recovery tank. Following surgery, fish were placed in fresh river water for 5 – 10 mins and monitored until normal stimulus responses resumed. They were then released at approximately the same area as initially captured.

Environmental monitoring

Environmental parameter data was obtained from various sources to track environmental conditions in the study area throughout the study period. Parameters were selected on the basis of previous relationships identified to influence the spatial use of fish species in multiple regions (Jackson et al. 2001; Paukert et al. 2004; Rogers et al. 2005). Daily mean temperatures were obtained from readings taken every 15 minutes by Hobo Pendant data loggers deployed on 15 of the receiver moorings in the study array. Moon illumination (McDowall 1969) was obtained from the time and date online archives (www.timeanddate.com). Water level data for the Detroit River was accessed from the National Oceanic and Atmospheric Administration (NOAA) monitoring station in Wyandotte, MI, located across from Fighting Island (www.tidesandcurrents.noaa.gov). Wind speeds for Grosse Ile, MI were obtained from the online archives of Weather Underground (www.wunderground.com) as a proxy for wind measures at Fighting Island due to the proximity of the two islands in the Detroit River. Daily mean flow data were obtained from flow readings taken in the Detroit River near Fort Wayne, MI every 6 minutes and reported online by the United States Geological Survey (USGS; www.nwis.waterdata.usgs.gov).

Data analysis

Tagged sunfish were identified as active resident fish within the array if detections were recorded on multiple receivers over time, indicating movement of the fish throughout the array. Detections recorded consistently on a single receiver for an extended period of time were assumed to be the result of either a dead fish or expelled tag (n = 1 pumpkinseed).

The complete detection database was initially filtered for false detections, i.e. detections that do not represent a tagged fish and are recorded when a receiver detects multiple tags around the same time or from noise signals that mimic a standard ping transmission sequence (Voegeli et al. 2001; Heupel et al. 2006), using the White-Mihoff Filtering Tool (White et al. 2014). This data-filtering tool identifies and removes potential false detections in two steps. First, detections isolated sequentially on either side by an hour were declared as false and removed from the detection database. Second, sequential detections with calculated transition speeds exceeding 0.3 m s^{-1}, the likely maximum sustained swimming speed for sunfish of the size used here (Jayne and Lauder 1993), were identified as false and removed from the database.

To examine patterns of activity throughout the day, the total number of detections at every hour throughout a 24 hr period was determined for both species. These values were then converted into a proportion of all detections for each species and plotted together. The proportion of all 50 m range test tag detections was also calculated by hour and plotted to establish if diel patterns were a result of array functionality throughout a 24 hr period, but represent detection range data available from October and November only because the 50 m tag was not within detection range prior to this date (see Supplemental material for details).

Habitat use patterns of each species were examined using Residence Index (RI) values that were calculated using the equation (Kessel et al. 2016):

$$\mathrm{RI} = \left(\frac{\text{\# of days with detections at receiver of interest}}{\text{total \# of days with detections at any receiver}}\right) \quad (1).$$

To identify overall spatial habitat preference of sunfish within the study site, the total RI of pumpkinseed and bluegill combined was calculated (RI_{total}). Species-specific RI values for pumpkinseed (RI_{PS}) and bluegill (RI_{BG}) were calculated to distinguish habitat use between the species. To investigate habitat variation between sides of the shipping channel through the study area, i.e. Fighting Island or LaSalle, capture location-specific

RI values were calculated for both species (RI_{FI} or RI_{LS}). ArcMap® (ver 10.3.1) was used to visualize RI results as graduated symbols, providing a visual depiction of spatial preference.

To verify that detection rates accurately represented sunfish activity rather than aspects of acoustic receiver performance, we monitored receivers in two ways; (a) by assessing individual receiver performance following the methods of Simpfendorfer et al. (2008), and (b) by performing controlled detection range testing. Briefly, there was no evidence of either sufficient noise in the system to consistently disrupt receiver performance or a large number of false sequences detected, i.e. those created by chance that do not match the programmed code sequences identifiable by the VR2W acoustic receivers. Additionally, the code detection efficiency was in the range of 25 – 50%, showing a general decrease over the study period but maintaining a range of values consistent with studies in other systems (see Supplemental material for details). Overall, there was no evidence of telemetry performance issues in the array that significantly impacted the detection data reported here.

To examine the patterns in activity levels of pumpkinseed and bluegill over the period of June – November 2015, five environmental variables were considered (water level, water temperature, moon phase, wind speed, and flow). Collinearity was tested using pairwise comparisons of the environmental variables to verify independence prior to inclusion in additional analyses (see Zuur et al. 2009 for details). All variables were found to be independent except water temperature and water level (pairwise correlation, cc = 0.9), as such temperature and level are considered as a single variable represented by water temperature readings in further analysis (Fig. S5). Generalized linear mixed models

(GLMM) were used to analyze the presence and absence of pumpkinseed and bluegill detections each day in relation to environmental parameters (e.g. Rhodes et al. 2009, Walsh et al. 2013), where daily presence of a species was defined by a minimum of one detection by that species in a day. The fixed parameters included in the models were daily means of water temperature (°C), moon phase (illumination scale from 0 to 1), wind speed ($km \cdot h^{-1}$), and flow ($m \cdot s^{-1}$) with sunfish ID included as a random effect. In movement data, such as telemetry, the location of an animal is, at least partially, dependent on where they were located in the previous time step leading to temporal autocorrelation (De Solla et al. 1999; Aarts et al. 2008). Temporal autocorrelation was tested by fitting separate non-autoregressive models to the bluegill and sunfish presence-absence data and applying the Breusch-Godfrey and Durbin-Watson autocorrelation tests. If temporal autocorrelation was detected for a species, a series of autoregressive (AR) models were run using different combinations of environmental variables included in the model and using increasing orders of residual error structure ('gls' function in the 'nlme' analysis package; Pinheiro et al. 2015). Models were tested up to the order where the Akaike Information Criteria (AIC) values began to increase. The best fitting autoregressive model was selected for each species on the basis of producing the lowest AIC. R version 3.2.0 (R Development Core Team 2015) was used for analyses and statistical significance was determined using $\alpha = 0.05$.

Results

Summary of tagged fish

The 29 sunfish tagged had similar body masses and lengths and did not differ between species (Table 1). Briefly, mean length of pumpkinseed was 155 mm ± 4.8 (mean ± 1 SE) as compared to 159 mm ± 4.3 for bluegill, while mean mass was 83.9 g ± 7.6 and 84.3 g ± 9.3 for pumpkinseed and bluegill, respectively. Based on the typical L_T of pumpkinseed and bluegill at sexual maturity (mean 100 – 104 mm depending on sex; Fox 1994), all individuals were considered to be reproductively mature for this study.

Detection summary

Over the study period, receiver detection performance varied, but in general was greatest during the first weeks of deployment and decreased later in the study period. Receiver performance fluctuated over the course of the observation period with peak efficiency levels during the first weeks of the study period and again after October, which approximately matched with observed patterns of broad scale seasonal macrophyte growth and die-off in the study area (see Supplemental material for detection range and receiver efficiency details). Correction of the data based on receiver performance was not done due to the spatial variation in detection range of receivers and daily variability in receiver performance that made it difficult to apply a correction that would appropriately fit the data.

Examination of detections from individual tagged sunfish revealed one pumpkinseed that was detected on various receivers for approximately 24 hours post-release and then detected at one receiver (M14) consistently for a period of 12 weeks.

Based on the criteria outlined above, this pumpkinseed was determined to be a dead fish or expelled tag. All detections related to this tag were removed from the analysis.

Between 24 June and 16 November 2015, a total of 37,804 detections from the 28 tagged sunfish IDs were recorded on the acoustic array – 27,094 pumpkinseed (n = 18) and 10,710 bluegill (n = 10) detections. The identification and removal of 5,485 (14.5% total detections) and 2,860 (7.6% total detections) false detections for pumpkinseed and bluegill, respectively, resulted in final databases with 21,609 and 7,850 pumpkinseed and bluegill, respectively, detections for a total of 29,459 used for analysis. Residence time of sunfish in the acoustic array, as measured by the number of days between the first and final detections, varied from 2 to 122 of the possible 146 days (mean = 22.8 $\pm$ 4.7). Residence time at receiver stations, as measured by the number of days with detections at a receiver, ranged from 7 to 117 days (mean = 39.2 $\pm$ 5.6) within the main array. A majority of detections for pumpkinseed (66.5%) and bluegill (52.0%) were recorded during nocturnal periods (Fig. 2).

Residence indexes (RI)

Across the entire study site the mean RI values were similar for both pumpkinseed (RI_{PS} = 0.21) and bluegill (RI_{BG} = 0.21; Fig. 3, Table 2), indicating that for any given receiver in the array a minimum of one tagged sunfish was detected on 21% of the study days. The RI values were greater for receivers located along the edge of the shipping channel (mean RI_{PS} = 0.36, RI_{BG} = 0.34) as compared to shallow, densely vegetated sites (mean RI_{PS} = 0.12, RI_{BG} = 0.13). Furthermore, when RI values were divided into tagging location relative to the channel, both pumpkinseed and bluegill were detected only in the shallow areas on the side in which they were tagged or by the channel receivers, e.g.

pumpkinseed tagged and released on the east side of the array were detected only in the shallow area to the east of the channel or by receivers lining both sides of the channel (see Fig. 3c).

Environmental factors and fish activity

The non-autoregressive generalized linear mixed model with the best AIC score included the environmental variables water temperature and moon illumination for pumpkinseed and water temperature, moon illumination, and flow for bluegill (Table 3a; Fig. 4). A significant level of autocorrelation was found in both non-autoregressive models of best fit (PS: Durbin-Watson $d = 0.603$, $P < 0.001$, Breusch-Godfrey $P < 0.001$; BG: Durbin-Watson $d = 0.594$, $P < 0.001$, Breusch-Godfrey $P < 0.001$). The best fitting first order autoregressive models revealed correlation between successive fish presence time steps of 72% and 73% for pumpkinseed and bluegill, respectively (Table 4b, PS $_{\Phi 1} = 0.718$; BG $_{\Phi 1} = 0.726$). The eighth order autoregression model Presence ~ Water Temp was the best fitting model for pumpkinseed (Table 3c, AIC = -651.447). Similarly, the seventh order autoregression model Presence ~ Water Temp was the best fitting model for bluegill (Table 3c, AIC = -220.220). In these models with just water temperature as a variable, the presence of pumpkinseed was related to temperature (Table 4c, $P = 0.002$), but not for bluegill (Table 4c, $P = 0.603$).

Discussion

Pumpkinseed and bluegill sunfish activity patterns in the Detroit River varied across both temporal and spatial scales, which differed from that described in small temperate lakes. Both species inhabited the shallow littoral flats on either side of the shipping channel but exhibited preference for different areas within the study site and did not make clear cross-channel movements into macrophyte areas. Sunfish activity within the study site was greater at higher water temperatures and levels, but not correlated with wind speed, moon illumination, or daily flow rates. Bluegill and pumpkinseed sunfish were both more active, 8 and 4 times respectively, at night than during hours of light. These results, which differ from those on sunfish from small lakes, have implications for trophic interactions and energy flow differences between various types of aquatic freshwater systems.

Both bluegill and pumpkinseed showed increased activity, as measured by the proportion of total detections for each species, during the overnight hours. The activity patterns of multiple fish species have been shown to change between periods of light and dark (Helfman 1981; Rooker and Dennis 1991; Shoup et al. 2004), including sunfish in temperate lakes (Keast and Welsh 1968). This diurnal variation in activity can occur through changes in where fish are found throughout the day (Robblee and Zieman 1984) or through their overall levels of activity (Boujard and Leatherland 1992). We argue that in this study greater detections at night were more likely due to increased sunfish activity given that the receivers at which sunfish were detected on did not vary between these periods, i.e., sunfish did not move to different receivers or areas with variable detection ranges at different times of the day (see Supplemental material, Table S2). As the detection rate of range tests tags did not vary across time of day, increased detections were assumed to relate to activity level and not a temporal detection bias (Fig. 2; Payne et al. 2010).

Bluegill in the Detroit River showed greater nocturnal activity compared to past descriptions in small lakes (Shoup et al. 2004), where this species has also been found to have no evidence of a diel pattern (Paukert et al. 2004). Bluegill activity in lakes has been linked to visual feeding of zooplankton suspended in the water column (Keast and Welsh 1968), whereas bluegill in the Detroit River have been shown to consume a benthic invertebrate diet (e.g. Paterson et al. 2006), which could explain this difference. Similar to studies in small lakes (Fish and Savitz 1983), pumpkinseed in the Detroit River were more active during the night. Given that sunfish are considered a visual predator (Gross and MacMillan 1981), higher activity at night would seem unlikely to be explained solely by feeding behaviour. As the diversity and number of predators in the Detroit River is larger than in small lakes (Francis et al. 2014), avoidance of visually-cued predators during the day, such as the largemouth bass (Savino and Stein 1982) common in this area of the Detroit River, may be related to a temporal shift in sunfish activity patterns.

Although both bluegill and pumpkinseed displayed greater activity at night, bluegill had a greater overall difference between night and day activity compared to pumpkinseed. This difference may reflect some temporal resource partitioning between these similar species, reducing overall interspecific completion with bluegill or other forage fish, such as the yellow perch (*Perca flavescens*). While it is not possible with the data collected here to distinguish between the role of predation and interspecific competition in the temporal activity patterns of sunfish, it is clear that sunfish within the Detroit River have distinct diel activity patterns and that these patterns differ from sunfish in smaller lake environments, where they are typically studied.

A large number of fish detections occurred at receivers positioned across the shipping channel relative to the tagging location of both species, i.e., east tagged fish detected on the west side of the shipping channel. It is possible that sunfish were crossing the channel on a regular basis, but we find this unlikely for two reasons. First, the acoustic detection range was significantly increased in the channel because there were no macrophytes. At the shallow habitat range test area immediately north of the focal study area (see Supplemental material for details), a cross-channel receiver detected 400 transmissions from a 180 kHz tag positioned 288 m away and 15 m within the peak vegetation line (14 September - 25 November 2015). In comparison, for this same tag there were 428 detections at a receiver positioned 75 m away but entirely within the vegetated area. Given the 250 – 300 m width of the channel through the study area and the deployment position of this range test tag, it is probable that tags could be detected on the opposite side of the channel without fish moving across or even directly into the channel. Second, if sunfish were regularly crossing the channel we would expect them to also be detected on the shallow receivers in both habitat patches, but we did not find this for either species, nor were there approximately equal RI values for receivers deployed in parallel along the length of the channel (Fig. 3). We conclude that despite the frequent detections of fish along the channel, it is most likely that sunfish are using the vegetation beds near the channels edge or making use of the channel margins rather than movements across the channel.

Within the shallow, highly vegetated areas of the study site, the sunfish species differed in residence patterns with bluegill occupying a broader area, including shoreline and channel areas, than pumpkinseed. Furthermore, on the east side of the shipping channel, where most sunfish were tagged (pumpkinseed = 10 of 18; bluegill = 8 of 10), pumpkinseed were more likely to reside in the northern half of the habitat, whereas bluegill were more frequently along the shoreline in the mid- and southern portions of the study area. The patterns observed here differ from habitat use predications based on temperate lakes where pumpkinseed and bluegill use the littoral and pelagic habitats differently based on foraging (Mittelbach 1984; Wainwright 1996); however, given the shift of bluegill to a benthic invertebrate diet in the Detroit River (Paterson et al. 2006), it is possible that these two species are now more directly competing for food resources and increasing the potential for interspecific resource competition. Therefore, in addition to temporal activity patterns that differ between the species, the overall residence patterns indicate the possibility of spatial habitat partitioning.

Pumpkinseed were more likely to be detected at higher water temperatures/levels, but there were no significant relationships between any of the measured environmental variables and bluegill detections. A variety of environmental variables have been shown to influence the habitat use of fish (e.g. Jackson et al. 2001; Ficke et al. 2007), but temperature is the most prominent environmental variable in aquatic studies due to the strong relationship with ecotherm physiology (e.g. Ficke et al. 2007). Indeed, temperature has been linked to habitat use of fish (e.g. Magnuson et al. 1990; Mohseni et al. 2003). However, temperature is not only linked to aspects of fish physiology (O’Hara 1968) but is also related to the broader composition and structure of aquatic communities. For example, vegetation in littoral macrophyte beds experience seasonal growth and decline cycles related to temperature and these changes in vegetation affect access to prey species (Crowder and Cooper 1982), predation risk (Savino and Stein 1989), and the overall structure of a habitat for forage fish. In addition, water level has been shown to effect fish species, including sunfish (Rogers et al. 2005), with higher levels increasing the potential habitat through vertical expansion of the water column (Keith 1975) and overall water quality (Gaboury and Palatas 1984). Consistent with the potential effects of environmental variables, pumpkinseed in the Detroit River were more likely to be detected in the system at higher temperatures and water levels, whereas bluegill detections were not related to any specific environmental variables measured, although their detection rates did decline over the observation period. Indeed, bluegill presence has previously been shown to not be specifically related to water temperature (Paukert et al. 2004). Further examination of environmental variables likely to affect forage fishes in the Detroit River, particularly sunfish, may best be directed towards the species-specific variation in relationships between water temperature and level relative to fish presence in littoral macrophyte beds.

Sunfish from both sides of the channel, including the smaller island side, were not observed to make regular movements across the shipping channel. Among the numerous effects anthropogenic activity may have had in the Detroit River, the channelization of the river to facilitate the movement of commercial vessels is possibly the most significant series of physical alterations to the structure of this aquatic community (Bennion and Manny 2011). Furthermore, a community-level survey of the shallow river margins (< 2.5 m depth) along the length of the Detroit River found that sunfish in general were typically found in areas of lower current and higher macrophyte density (Lapointe et al. 2007). It is likely that sunfish, adapted for short bursts of swimming activity (Jones et al. 2007; Kendall et al. 2007; Wilson and Godin 2010), avoid the increased flow or predation risk associated with the shipping channels throughout the Detroit River (Manny and Kenaga 1991; MacLennan et al. 2003) and could be subject to habitat fragmentation even on the relatively small scale considered here. The altered landscape of the Detroit River may influence the extent of genetic connectivity among populations of fishes separated by man-made features, e.g. channelization, which can impact the persistence and organization of these populations (Leclerc et al. 2008). Therefore, shallow habitats with lower flow rates and dense vegetation are important for at least some native forage fish species, and the overall health and connectivity of these habitats should be factored into community-level assessment and restoration projects.

The distinct river morphology and depth profile of the Detroit River likely influenced the available habitat for bluegill and pumpkinseed sunfish in comparison to populations from smaller temperate lakes, where these species are most commonly studied. To further understand the impacts of urbanization on freshwater fish, particularly related to channelization and habitat fragmentation for small fishes, telemetry studies in more urbanized areas, for example with hard surfaced shorelines, are required. Through the use of acoustic telemetry to monitor residence patterns over an extended period of time we have shown that within a large connecting channel there is not only distinct habitat use between shallow and open-water areas by two sympatric sunfish, but that they may further partition the available habitat through both temporal activity levels and spatial distribution.

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Table 1. Summary of characteristics of pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*) tagged on 23 – 24 June and 6 August 2015; n is the number of individuals and TL is total length (± SE).

Tagging group	n	Mean TL (mm)	TL range (mm)	Mean mass (g)	Mass range (g)
Pumpkinseed	19	155 ± 5	120 – 186	83.9 ± 7.6	32 – 150
Bluegill	10	159 ± 4	140 – 178	84.3 ± 9.3	56 – 126
Total	29	156 ± 3	120 – 186	84.1 ± 5.8	32 – 150

Table 2. Residence Index (RI) values (mean ± SE) for pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*) in a 650 m section of the Detroit River with 26 VR2W 180 kHz receivers. For each receiver, an individual RI value was calculated and is reported as part of the total array or divided into groups based on location within the study site.

Section	Pumpkinseed (RI_{PS})			Bluegill (RI_{BG})		
	Total	East tagged (n = 11)	West tagged (n = 8)	Total	East tagged (n = 8)	West tagged (n = 2)
Full array (n = 26)	0.21 ± 0.04	0.10 ± 0.02	0.17 ± 0.04	0.21 ± 0.03	0.15 ± 0.03	0.16 ± 0.04
All channel (n = 10)	0.36 ± 0.08	0.11 ± 0.04	0.34 ± 0.08	0.34 ± 0.06	0.25 ± 0.05	0.30 ± 0.09
East channel (n = 5)	0.49 ± 0.13	0.19 ± 0.07	0.47 ± 0.13	0.45 ± 0.07	0.30 ± 0.09	0.48 ± 0.13
West channel (n = 5)	0.23 ± 0.08	0.03 ± 0.02	0.21 ± 0.09	0.23 ± 0.07	0.20 ± 0.06	0.12 ± 0.06
All shallow (n = 16)	0.12 ± 0.02	0.10 ± 0.03	0.06 ± 0.03	0.13 ± 0.02	0.09 ± 0.03	0.08 ± 0.03
East shallow (n = 10)	0.10 ± 0.02	0.16 ± 0.03	0.00 ± 0.00	0.13 ± 0.03	0.14 ± 0.03	0.00 ± 0.00
West shallow (n = 6)	0.15 ± 0.05	0.00 ± 0.00	0.15 ± 0.05	0.13 ± 0.03	0.00 ± 0.00	0.22 ± 0.05

Table 3. Generalized linear mixed models constructed to estimate the influence of environmental parameters on the daily detections of pumpkinseed (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*). Models are separated by species and grouped by a) non-autoregressive b) first order autoregressive and c) best fitting order autoregressive. Models with the lowest AIC value (bold) indicate the best fitting and most parsimonious models. Explanatory variables include daily water temperature, wind speed, moon illumination, and flow.

Pumpkinseed		**Bluegill**	
a) Non-autoregressive Models	AIC	a) Non- autoregressive Models	AIC
Water Temp + Wind Speed + Moon Illum + Flow	1252.876	Water Temp + Wind Speed + Moon Illum + Flow	909.659
Water Temp + Moon Illum + Flow	1251.792	Water Temp + Moon Illum + Flow	**908.038**
Water Temp + Moon Illum	**1251.648**	Water Temp + Moon Illum	909.512
Water Temp	1285.010	Water Temp	936.712
b) AR1 Models		b) AR1 Models	
Water Temp + Wind Speed + Moon Illum + Flow	-0.957	Water Temp + Wind Speed + Moon Illum + Flow	6.846
Water Temp + Wind Speed + Flow	-48.149	Water Temp + Wind Speed + Flow	-32.306
Water Temp + Wind Speed	-69.227	Water Temp + Wind Speed	-50.273
Water Temp	**-83.351**	Water Temp	**-63.512**
c) AR8 Models		c) AR7 Models	
Water Temp + Wind Speed + Moon Illum + Flow	-560.564	Water Temp + Wind Speed + Moon Illum + Flow	-152.722
Water Temp + Wind Speed + Flow	-615.632	Water Temp + Wind Speed + Flow	-186.583
Water Temp + Wind Speed	-637.077	Water Temp + Wind Speed	-206.557
Water Temp	**-651.447**	Water Temp	**-220.220**

Table 4. Environmental parameter estimates and summary statistics for the most parsimonious models fit to the daily presence of pumpkinseed (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*) using a) non-autoregression (non-AR) b) first order autoregression (AR1) and c) best fitting order autoregression (AR7 for pumpkinseed; AR8 for bluegill). AR $_{\Phi's}$ are the autoregression parameters.

Pumpkinseed					**Bluegill**				
Coefficients	**Estimate**	**SE**	***t*-value**	***P*-value**	**Coefficients**	**Estimate**	**SE**	***t*-value**	***P*-value**
a) Best Non-AR Model:					a) Best Non-AR Model:				
Presence ~ Water Temp + Moon Illum					Presence ~ Water Temp + Moon Illum + Flow				
Intercept	-8.420	0.857	-9.827	<0.001	Intercept	0.787	2.908	0.270	0.787
Water Temp	0.243	0.023	10.607	<0.001	Water Temp	0.130	0.025	5.317	<0.001
Moon Illum	0.007	0.209	0.032	0.974	Moon Illum	0.240	0.250	0.956	0.339
					Flow	-0.001	<0.001	-2.119	0.034
Durbin-Watson	Breusch-Godfrey				Durbin-Watson	Breusch-Godfrey			
$d = 0.603$	$p < 0.001$				$d = 0.594$	$p < 0.001$			
$p < 0.001$					$p < 0.001$				
b) Best AR1 Model: Presence ~ Water Temp					b) Best AR1 Model: Presence ~ Water Temp				
Intercept	-0.111	0.059	-1.871	0.061	Intercept	-0.050	0.083	-0.606	0.545
Water Temp	0.013	0.003	4.412	0.000	Water Temp	0.010	0.004	2.378	0.018
AR $_{\Phi 1}$	0.718				AR $_{\Phi 1}$	0.726			
c) Best AR8 Model: Presence ~ Water Temp					c) Best AR7 Model: Presence ~ Water Temp				
Intercept	-0.040	0.077	-0.514	0.607	Intercept	0.103	0.109	0.947	0.344
Water Temp	-0.011	0.004	3.053	0.002	Water Temp	0.003	0.005	0.520	0.603

AR Φ's	0.327, 0.198, 0.128, 0.091, 0.013, 0.016, 0.072, 0.050, 0.025	AR Φ's	0.482, 0.112, 0.027, 0.152, -0.008, 0.064, 0.066

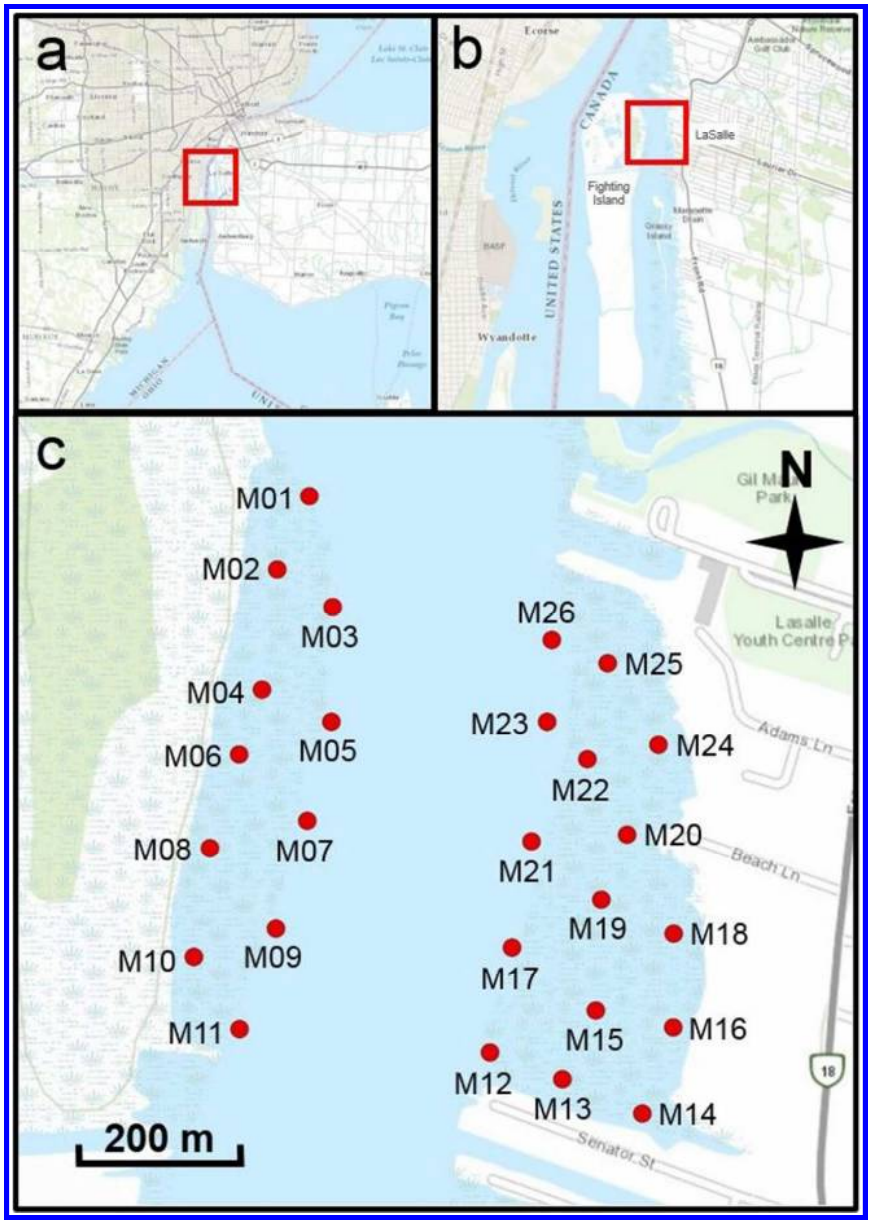
Figure Captions

Figure 1. Detroit River study site (42°23N, 83°10W); **a** location of study (*box*) within the Huron-Erie Corridor in the Laurentian Great Lakes; **b** location of study (*box*) relative to Fighting Island and LaSalle, Ontario, Canada; **c** acoustic array where *circles* represent receiver stations and corresponding classification number. Map source: United States Environmental Protection Agency.

Figure 2. Proportion of detections for pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*) separated by hour in Eastern Standard Time. The *blue line* represents the proportion of bluegill detections and the *orange line* represents the proportion of pumpkinseed detections. The *dotted line* represents the proportion of 50 m range test tag detections (data available only after 29 September 2015 due to range limits before that time). The *white area* indicates the mean diurnal period over the course of the study and the *dark grey area* indicates the mean nocturnal period. The *light grey areas* represent the range of sunrise and sunset times during the study period.

Figure 3. Residence Index (RI) by acoustic receiver station across the entire study period (24 June 2015 – 16 November 2015). *Orange circles* represent mean RI for pumpkinseed (RI_{PS}); **a** total tagged individuals (n = 18); **c** east capture location (n = 10); **e** west capture location (n = 8). *Blue circles* represent mean RI for bluegill (RI_{BG}); **b** total tagged individuals (n = 10); **d** east capture location (n = 8); **f** west capture location (n = 2). Map source: United States Environmental Protection Agency.

Figure 4. Presence and absence in relation to various factors. *Blue dots* represent bluegill detections and *orange dots* represent pumpkinseed detections. Vertical *red lines* indicate the date of tagging and release for individual fish. *Black lines* represent different environmental variables monitored during this period; **a** receiver array performance; **b** water level (IGLD); **c** water temperature (^{o}C); **d** moon illumination (%); **e** wind speed (km h^{-1}); **f** flow (m s^{-1}).



Detroit River study site (42°23N, 83°10W); **a** location of study (*box*) within the Huron-Erie Corridor in the Laurentian Great Lakes; **b** location of study (*box*) relative to Fighting Island and LaSalle, Ontario, Canada; **c** acoustic array where *circles* represent receiver stations and corresponding classification number.

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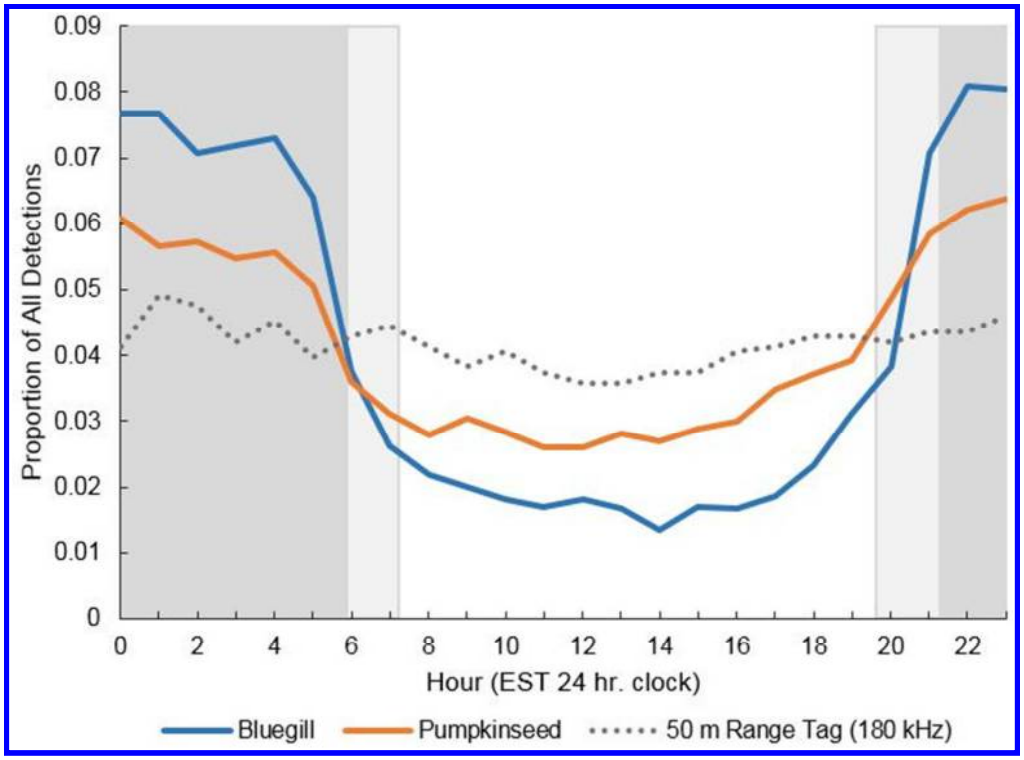

Proportion of detections for pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*) separated by hour in Eastern Standard Time. The *blue line* represents the proportion of bluegill detections and the *orange line* represents the proportion of pumpkinseed detections. The *dotted line* represents the proportion of 50 m range test tag detections (data available only after 29 September 2015 due to range limits before that time). The *white area* indicates the mean diurnal period over the course of the study and the *dark grey area* indicates the mean nocturnal period. The *light grey areas* represent the range of sunrise and sunset times during the study period.

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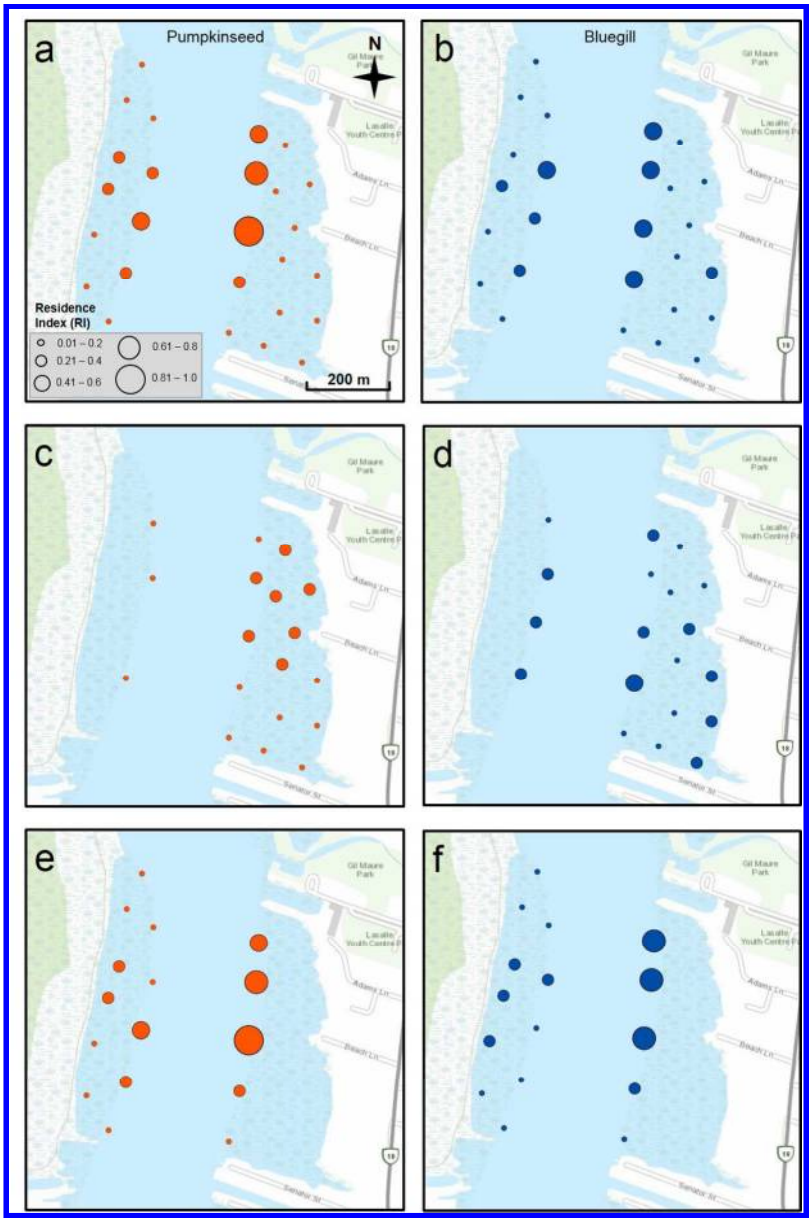

Residence Index (RI) by acoustic receiver station across the entire study period (24 June 2015 – 16 November 2015). *Orange circles* represent mean RI for pumpkinseed (RI_{PS}); **a** total tagged individuals (n = 18); **c** east capture location (n = 10); **e** west capture location (n = 8). *Blue circles* represent mean RI for bluegill (RI_{BG}); **b** total tagged individuals (n = 10); **d** east capture location (n = 8); **f** west capture location (n = 2).

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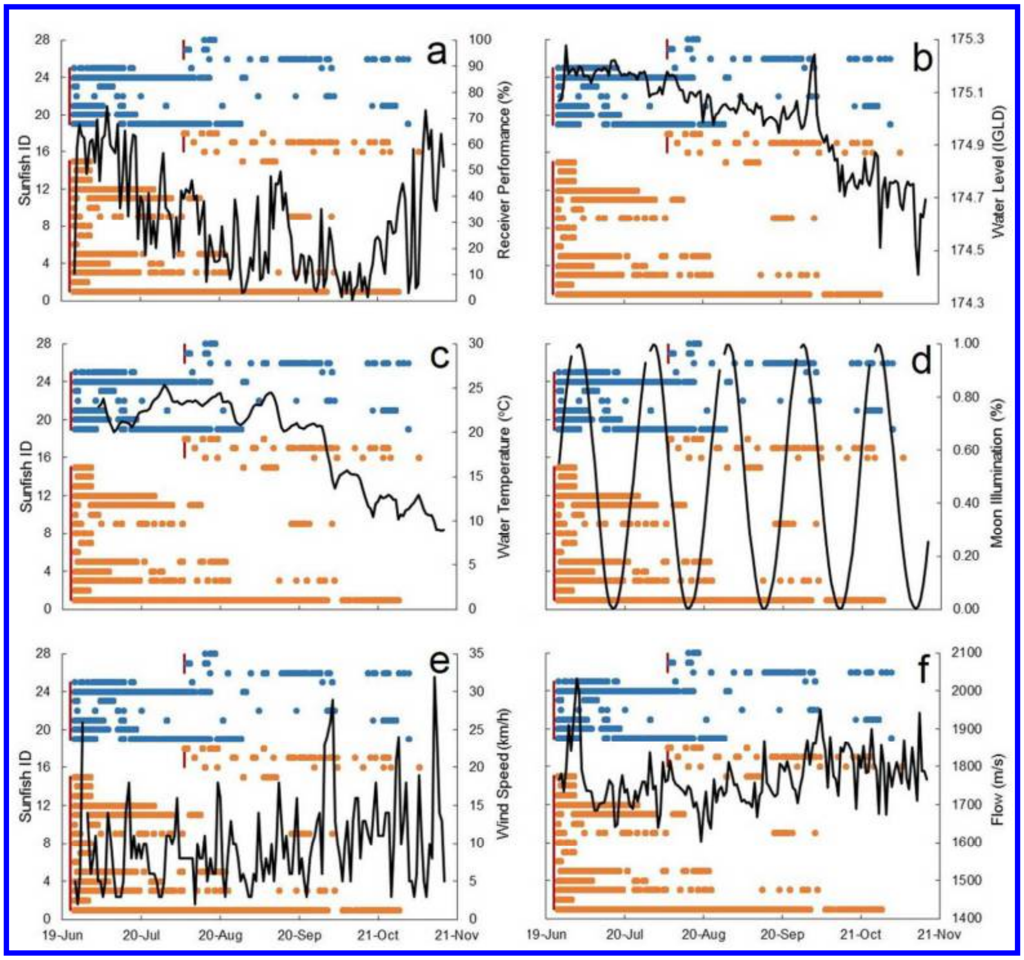

Presence and absence in relation to various factors. *Blue dots* represent bluegill detections and *orange dots* represent pumpkinseed detections. *Vertical red lines* indicate the date of tagging and release for individual fish. *Black lines* represent different environmental variables monitored during this period; **a** receiver array performance; **b** water level (IGLD); **c** water temperature (°C); **d** moon illumination (%); **e** wind speed (km h^{-1}); **f** flow (m s^{-1}).

212x198mm (150 x 150 DPI)